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Wetness modulates the effects of grazing on net ecosystem productivity in global grasslands

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This study uses **convincing** modeling methods and analyses of rich behavioral datasets to investigate the role of attention in value-based decision making; for instance, as when choosing between two snacks. The results are **valuable**, as they challenge existing theories that assume that paying attention to an available option biases the eventual choice toward that option. The results suggest that the correlation between attention and decision-making is formed largely after and not before the (internal) choice process has terminated, a finding that offers an intuitively appealing rethinking of how attention and decision-making processes interact during value-based choices.

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Abstract

Overgrazing has caused widespread global concern. However, how grazing intensity affects ecosystem carbon dioxide (CO₂) fluxes with wetness fluctuations in grasslands at a global scale remains poorly understood. Here we measured ecosystem CO₂ fluxes covering the 7th to 11th years of a continuous grazing experiment in a typical steppe, and conducted a meta-analysis of 585 observations by collecting relevant data in global grasslands. Our experimental results showed that mean gross primary productivity (GPP) and ecosystem respiration (ER) were decreased under heavy grazing (HG) compared with control without grazing (CK), whereas net ecosystem productivity (NEP) was not different between HG and CK in the typical steppe. The NEP was higher under light grazing in the wetter years, but it was not different between LG and CK under drier years in the typical steppe. In contrast, grazing decreased GPP, ER and NEP, respectively, in global grasslands. Both our field experiment and the meta-analysis revealed that the response of NEP to light grazing was linearly correlated with the wetness index, which may be mediated by greater plant relative growth rate in wetter years. Higher wetness and aboveground biomass (AGB) increased the response of NEP to grazing in global grasslands. However, heavy grazing reduced NEP and AGB even under higher wetness indices in global grasslands, resulting from a loss of their resilience in long-term heavy grazing. These findings indicate that light grazing appears to be a promising management to promote plant relative growth rate and CO₂ flux sequestration. Furthermore, major drivers influencing ecosystem CO₂ fluxes in response to grazing were

aboveground biomass, grazing intensity and wetness index. Overall, this study provides a global perspective on the response of ecosystem CO₂ fluxes to grazing intensity and improves our knowledge of the factors influencing the response of ecosystem CO₂ fluxes to grazing intensity.

1. Introduction

Grasslands play a vital role in livestock production, promoting carbon (C) sequestration and regulating climate change (Heimann & Reichstein, 2008 [↗](#); Zhou et al., 2017 [↗](#)). Globally, grassland ecosystems cover approximately one fifth of the world land surface and contain about 20-30% of the global pool of soil organic C (Du et al., 2022 [↗](#)). Grazing is a widespread land-use activity that significantly alters terrestrial C dynamics (He et al., 2020 [↗](#); Zhou et al., 2025 [↗](#)). Up to 49.25% of grassland area has degraded worldwide, around 5% experiencing severe degradation (Gang et al., 2014 [↗](#)). Grassland degradation is influenced by a multitude of driving factors, such as overgrazing and precipitation limitation (Sloat et al., 2018 [↗](#)). Furthermore, the C balance of grasslands is also increasingly influenced by changes in grazing management practices and water availability (Hilker et al., 2014 [↗](#); Lemoine et al., 2016 [↗](#); Ren et al., 2025 [↗](#)). Overgrazing and drier conditions could potentially drive grasslands from acting as C sinks to C sources (Hao et al., 2018 [↗](#); Morgan et al., 2016 [↗](#); Shao et al., 2013 [↗](#)).

Gross primary productivity (GPP) and ecosystem respiration (ER) are critical processes governing C sequestration and emission in terrestrial ecosystems (Chen et al., 2023 [↗](#); Knauer et al., 2023 [↗](#)). Net ecosystem productivity (NEP) is the balance between ecosystem C uptake and release, and serves as a key indicator of the net C exchange (Niu et al., 2010 [↗](#); Zhang et al., 2024 [↗](#)). Grazing influences NEP by altering GPP and ER (Fig. 1 [↗](#)). Thus, accurately assessing ecosystem carbon dioxide (CO₂) fluxes (GPP, ER and NEP) in grasslands is essential to the terrestrial C cycle at local, regional and global scales. However, current evidence on the effect of grazing on ecosystem CO₂ fluxes in grasslands remains inconsistent, with studies reporting both positive (Chang et al., 2020 [↗](#); Du et al., 2022 [↗](#)) and negative (Liu et al., 2020 [↗](#); Wang et al., 2023 [↗](#); Zhu et al., 2015 [↗](#)) effects. For instance, some studies demonstrated that grazing decreased GPP and ER (Nakano et al., 2020 [↗](#); Qi et al., 2024 [↗](#); Wang et al., 2025 [↗](#)), while others reported an increase or no difference in GPP or ER (Chang et al., 2020 [↗](#); Luo et al., 2015 [↗](#); Shi et al., 2022a [↗](#)). Similarly, some studies investigated that grazing significantly reduced NEP (Wang et al., 2023 [↗](#); Zhu et al., 2015 [↗](#)), while others reported an increase or no difference in NEP under grazing (Du et al., 2022 [↗](#); Gomez-Casanovas et al., 2018 [↗](#); Yu et al., 2025 [↗](#)). The variations in the responses of ecosystem CO₂ fluxes are likely driven by differences in grazing intensities, climatic variations, livestock and grassland types (Hou et al., 2016 [↗](#); Wang et al., 2023 [↗](#); Xiao et al., 2011 [↗](#); Zhu et al., 2015 [↗](#)).

The effects of grazing intensities on ecosystem CO₂ fluxes in global grasslands were also varied in different studies (Table S1; Jiang et al., 2020 [↗](#); Rong et al., 2017 [↗](#); Zhang et al., 2022 [↗](#)). Specifically, heavy grazing usually reduced the GPP, ER and NEP (Ju et al., 2024; Rong et al., 2017 [↗](#); Zhang et al., 2022 [↗](#)), but a meta-analysis also reported the response of NEP was increased in Chinese grasslands (Jiang et al., 2020 [↗](#)). Generally, light grazing can enhance NEP by promoting plant regeneration and improving photosynthetic efficiency, whereas moderate to heavy grazing tends to reduce NEP, largely as a result of decreased vegetation coverage and plant biomass (Yu et al., 2025 [↗](#)). Conversely, a meta-analysis showed that the response of NEP was decreased under light and moderate grazing (Zhang et al., 2022 [↗](#)). However, it was reported that moderate grazing led to the highest NEP (Zhu et al., 2015 [↗](#)). These conflicting results underscore the complex responses of ecosystem CO₂ fluxes in grasslands to grazing and highlight the necessity to identify key factors controlling ecosystem CO₂ flux dynamics under grazing management. This understanding is essential for accurately modelling and predicting grassland C dynamics under global change.

Many studies have demonstrated that yearly variation in grassland NEP can be substantial, primarily driven by fluctuating climatic conditions, as they can directly regulate vegetation growth via altering soil moisture and temperature (Rong et al., 2017 [↗](#); Wayne Polley et al., 2008 [↗](#); Shen et al., 2016 [↗](#)). Annual precipitation is one of the climatic parameters, while the wetness index (WI) serves as a more integrative climatic indicator that incorporates both

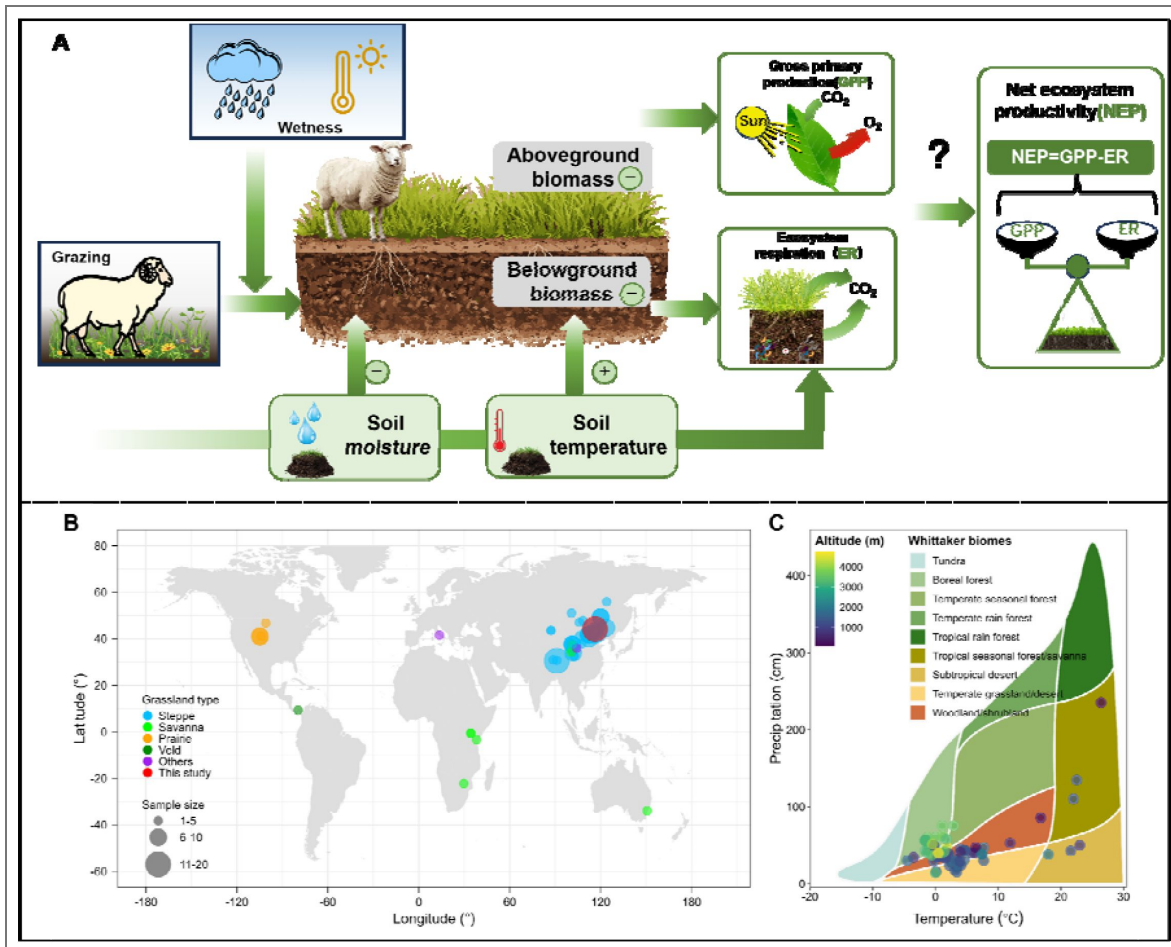


Figure 1. Conceptual illustration of how grazing with wetness fluctuation would affect net ecosystem productivity (A), and geographic (B) and climatic distributions of data (C) included in this meta-analysis.

precipitation and temperature, thereby reflecting the overall water surplus or deficit (Song et al., 2019). A higher wetness index ($WI > 30$) indicates sufficient water availability for plant growth, whereas a lower wetness index ($WI \leq 30$) suggests the water availability may be limited (Botzan et al., 1998). Considerable uncertainty remains regarding how NEP responds to grazing under different water conditions. Although evidence suggested that, under wet year, grazing significantly increased NEP; under dry year, grazing suppressed NEP and can even turn NEP negative (Shao et al., 2013). In general, grazing tends to have a less suppressive effect on NEP under wet than dry conditions (Okach et al., 2019; Zhou et al., 2019). For example, heavy grazing consistently reduced NEP, with a more pronounced decline occurring during dry years in a desert steppe (Jin et al., 2023). In addition, overgrazing led to decoupling of precipitation patterns and ecosystem carbon exchange in the desert steppe, primarily by altering plant community composition (Wang et al., 2023). However, it remains unclear how NEP responds to grazing intensities under water availability fluctuations across global grasslands.

Previous studies on the effects of grazing intensities on ecosystem CO_2 fluxes have been constrained by limited spatial and temporal scales, which has led to an incomplete understanding of how different grazing intensities influence ecosystem CO_2 fluxes with changes of annual wetness index. In this study, we investigated the effects of grazing intensities on ecosystem CO_2 fluxes by combining a long-term (7-11 years) field experiment conducted in a typical steppe and a meta-analysis of global grasslands. The objectives of this study were to: (i) investigate the effects of grazing intensity with annual wetness fluctuations on ecosystem CO_2 fluxes (GPP, ER and NEP) covering the 7th to 11th years of a continuous grazing experiment in a typical steppe as well as the meta-analysis in global grasslands; (ii) explore how environmental factors (particularly wetness index, soil moisture and temperature, grazing duration and grazing intensity) regulate the effects of grazing on ecosystem CO_2 fluxes. We hypothesized that: (H1) the response of net ecosystem productivity to grazing (including light, moderate and heavy grazing) would shift from negative to positive with increasing wetness index; (H2) aboveground biomass (AGB), grazing intensity and wetness index would act as key factors regulating the responses of ecosystem CO_2 fluxes to grazing, with their responses intensifying with AGB, grazing intensity and wetness index.

2. Materials and methods

2.1. Experimental site

The grazing experiment was conducted at Xilinhot National Climate Observatory (44°12' N, 116°19' E, 1129 m above sea level), in the middle part of Inner Mongolian typical steppe in China. The average annual precipitation was 291 mm from 2019 to 2023, with average precipitation in the growing season (May to September) varying from 168 to 325 mm (Fig. S1). The average mean air temperature was 3.9 °C (from 2019 to 2023). The soil is classified as a Haplic Calcisol based on the FAO soil classification system or a Calcic-Orthic Aridisol based on the USDA soil classification system (Liang et al., 2021). The vegetation community is dominated by *Stipa grandis* P. Smirn (perennial bunchgrass) and *Leymus chinensis* Trin. Tzvel (perennial rhizomatous grass) (Wu et al., 2024).

2.2. Experimental design

The grazing experiment was initiated in 2013 and was based on a randomized design (Fig. S2). There were four treatments with three replicates: control without grazing (CK), light grazing (LG, 0.75 sheep $ha^{-1} year^{-1}$), moderate grazing (MG, 1.5 sheep $ha^{-1} year^{-1}$) and heavy grazing (HG, 3 sheep $ha^{-1} year^{-1}$) conducted in plots with 1.44 ha ($120 \times 120 m^2$) established in the research station (Fig. S2). Two-year-old sheep similar in size were selected to use for grazing from May to September in each year. Sheep were grazing from 7:00 AM to 6:00 PM each day, and then gathered into an enclosure at night (Liang et al., 2021).

2.3. Measurement of ecosystem CO₂ fluxes

Ecosystem CO₂ fluxes were measured using a transparent chamber (0.5 × 0.5 × 0.8 m³) connected to an infrared gas analyzer (LI-8100, Lincoln, NE, USA). To ensure an airtight seal during measurements, the junction between the chamber bottom and the aluminum base was secured with tapes. After positioning the chamber, the enclosed air was continuously mixed by two fans in the chamber. The CO₂ concentrations were recorded 12 times at 10-second intervals over a 2-minute period. The NEP was then determined from the rate of CO₂ concentration change, combined with chamber volume and headspace temperature data. A positive NEP value indicated net ecosystem CO₂ uptake, whereas a negative value denoted net ecosystem CO₂ release. Following each NEP measurement, the chamber was removed to vent the headspace and then covered with a dark cloth to inhibit photosynthesis before being repositioned on the same base for ER measurement. Both the NEP and ER were measured throughout the growing seasons from 2019 to 2023, corresponding to the 7th to 11th years of grazing. The GPP was thus calculated as the sum of NEP and ER using data collected over this five-year period. All gas exchange measurements were conducted on sunny days between 9:00 and 11:00 AM, with a frequency of three times per month.

2.4. Climate conditions and soil microclimate

The mean annual precipitation (MAP) and mean annual temperature (MAT) for the study area from 2019 to 2023 were obtained from the China Meteorological Data Service Center (<http://data.cma.cn/>). The De Martonne wetness index (WI) was calculated as follows (Song et al., 2019):

$$\text{Wetness index (WI)} = \frac{MAP}{MAT + 10} \quad (1)$$

Soil temperature and moisture (hereafter referred to as soil moisture) at a depth of 0-10 cm were measured using the probes of the LI-8100 system. Measurement sites for soil temperature and moisture were selected near the collars randomly placed in the plots. They were investigated synchronized with the measurements of ecosystem CO₂ fluxes.

2.5. Plant sampling and analyses

To track changes in plant AGB, vegetation surveys were conducted in August each year from 2019 to 2023. Specifically, in each plot, five 1 × 1 m² quadrats were randomly placed. All aboveground biomass within these quadrats was clipped at ground level and then oven-dried at 65 °C for 48 h to determine the community-level dry biomass. Belowground biomass (BGB) was quantified by collecting root biomass using soil cores. Each September from 2019 to 2023, two soil cores with a diameter of 7 cm were collected from each 1 × 1 m² quadrat at depths of 0-30 cm. Subsequently, the belowground parts were extracted from soil by rinsing them in water, and then oven-dried at 65 °C for 48 h to obtain the dry weight.

The relative growth rate (RGR) was defined as the ratio of aboveground biomass regeneration to the number of days between two consecutive grazing events and was calculated by Eq. (2) (Zong & Shi, 2019):

$$RGR = \frac{(AGBE_{i+1} - AGB_i)}{\Delta t} \quad (2)$$

where $AGBE_{i+1}$: the aboveground biomass inside the caged plots after the (i+1)-th grazing round, AGB_i : the remaining aboveground biomass after the i-th grazing, Δt : the number of days between the i-th and (i+1)-th grazing rounds.

Aboveground net primary productivity (ANPP) was estimated as the sum of the total herbage consumed by livestock throughout the growing season and the AGB measured at the end of the final grazing rotation of the season.

2.6. Data Analysis

All the analyses were conducted using the R (version 4.4.3) (R Core Team, 2023 [↗](#)). Annual mean values were calculated for GPP, ER, NEP, AGB, BGB, root shoot ratio (R/S), soil temperature, and soil moisture from 2019 to 2023. Differences across years and among treatments within each year were examined using the Least Significant Difference (LSD) test. Response ratios of AGB, BGB, NEP, and GPP were calculated based on Eq. (3). Additionally, linear regression analysis was conducted using the “*lm*” function to evaluate the relationships of GPP, NEP, AGB, BGB, and RGR with WI.

$$\ln RR = \ln \left(\frac{X_t}{X_c} \right) = \ln (X_t) - \ln (X_c) \quad (3)$$

where X_t and X_c are the mean values of the abovementioned indicators for the grazing (t) and control (c) treatments, respectively.

The repeated measures ANOVA (the *ezANOVA* function of the “*ez*” R package) was used to examine the effects of grazing treatment and sampling years on ecosystem CO₂ fluxes (GPP, ER, and NEP), microclimatic variables (soil temperature and moisture), and plant biomass parameters (AGB, BGB, and R/S) across the five-year study period from 2019 to 2023.

We also conducted a random forest model to identify the significant environmental predictors of GPP, ER, NEP, AGB and BGB. The random forest model was implemented in R using the “*randomForest*” and “*rfPermute*” packages. In this model, the importance of each predictor was evaluated based on the percentage increase in the mean squared error (MSE) when that predictor was permuted; a higher MSE value indicated greater importance of the factor. The MSE values for each decision tree, based on out-of-bag estimates from the random forest model, were generated using the “*rfPermute*” package to assess the relative importance of the predictor variables (Liao et al., 2024 [↗](#)).

2.7. Meta-analysis of grazing experiments in global grasslands

To assess the effects of grazing on GPP, ER, and NEP in global grasslands, we conducted a systematic literature search for relevant papers published up to June 8, 2025, using the Web of Science (<http://apps.webofknowledge.com/> [↗](#)) and China National Knowledge Infrastructure (CNKI, <https://www.cnki.net> [↗](#)). The keywords and terms used were (“grazing” OR “stocking” OR “livestock” OR “grazing intensity”) AND (“net ecosystem productivity” OR “net ecosystem exchange” OR “gross ecosystem productivity” OR “ecosystem respiration” OR “soil carbon flux” OR “soil CO₂” OR “soil carbon flux” or “soil carbon emission”). Relevant studies were selected based on the following criteria: (a) Studies were conducted using simulating grazing experiments, and studies with trampling and mowing were excluded. (b) The control and grazing plots were under similar conditions, such as dominant species, community composition, soil type and climate. (c) Studies involving additional treatments (e.g., fertilization, experimental warming, or precipitation manipulation) were excluded, and only the control and grazing treatments were included in our data. (d) The mean and sample size for any measurements of GPP, ER, and NEP under both grazing and control conditions must be reported. Finally, 62 published papers with 585 observations of GPP, ER, and NEP responses ($n = 161, 249, \text{ and } 175$, respectively) were selected (Fig. 4 [↗](#)), and the geographical location of these observations were presented in Fig. 1 [↗](#). Meanwhile, the study site, elevation, MAP, MAT, and grazing intensity from the selected papers were recorded. The wetness indices based on MAP and MAT of each site were calculated according to Eq. (1). Where available, data for soil temperature, soil moisture, AGB, BGB, and R/S were also recorded.

In addition, to better explore the effects of grazing intensity and environmental factors on ecosystem CO₂ fluxes, the data was classified into different subgroups by grazing intensity (LG, MG, and HG), mean annual temperature (≤ 5 °C and >5 °C), wetness index (≤ 30 and > 30), and precipitation (≤ 400 mm and > 400 mm).

The effect size of grazing on each variable was quantified using the natural logarithm of response ratios ($\ln RR$) based on Eq. (3) (Feng et al., 2023 [↗](#)).

The weighing of the i th study (W_{RR}) was calculated as (Pittelkow et al., 2015):

$$W_{RR} = \frac{(N_C \times N_T)}{(N_C + N_T)} \quad (4)$$

where N_T and N_C are the replicate numbers of treatment and control, respectively.

A linear mixed-effects model, with ‘study’ included as a random factor, was employed to estimate the weighted response ratio (RR_{++}) across studies or within a specific group.

$$RR = \beta_0 + \pi_{\text{study}} + \varepsilon \quad (5)$$

where β_0 is the coefficient, π_{study} denotes the random effect associated with ‘study’ (accounting for autocorrelation among observations from the same study), and ε corresponds to the residual sampling error. When the assumption of normality was violated, bootstrapping with 999 iterations was performed using the BOOT package to derive the 95% confidence interval (CI) for each RR_{++} (Chen et al., 2021). The percentage change (%) of the response ratio was calculated as follows:

$$\text{Percentage Change} = (e^{RR_{++}} - 1) \times 100\% \quad (6)$$

The $\ln RR_{++}$ was considered statistically significant if its 95% confidence interval (CI) did not overlap zero (Chen et al., 2021).

The random forest model was conducted using “*randomForest*” and “*rfPermute*” packages to identify the relative importance of the predictor variables (wetness index, grazing duration and intensity, the responses of soil moisture and temperature and livestock types) of GPP, ER, NEP, AGB and BGB in the meta-analysis (Liao et al., 2024).

3. Results

3.1 Grazing intensity effects on ecosystem CO₂ fluxes and plant biomass

Continuous heavy grazing reduced the mean GPP by 27.31% and the mean ER by 28.05% in the grazing experiment; however, NEP did not differ between HG and CK (Fig. 2). The mean GPP and ER were decreased by 17.15% and 19.48%, respectively, in MG than in CK, but NEP was not different between MG and CK. The mean ER was decreased by 19.48% and 28.05%, respectively, in MG and HG than in LG. The mean NEP was decreased by 43.55% in HG than in LG, but was not different among LG, MG and CK. The GPP and NEP were 29.27% and 85.83% higher, respectively, in LG than in CK, but the ER was not different in 2020, the year with the highest precipitation and WI among the five years (Fig. S1 and 2). The mean aboveground and belowground biomass was decreased by 34.96% and 19.44%, respectively, in HG than in CK, but the mean root shoot ratio was increased by 30.57% in HG than in CK (Fig. 2; $P < 0.05$).

Wetness was the most important predictor of NEP, while grazing intensity was the most important predictor of GPP and ER, revealing a strong coupling between CO₂-driven changes in wetness index and grazing intensity (Fig. S3). Grazing intensity and duration were also the important predictors influencing AGB and BGB. The linear regression analysis showed that overall grazing as well as light grazing stimulated the responses of GPP and NEP with increasing wetness index (Fig. 3; $P < 0.05$). This relationship could be explained by the significant positive correlation between NEP and both ANPP and RGR (Fig. S4). In the wettest year of 2020, the relative growth rate peaked relative to other years, reaching levels 3.16, 2.76 and 1.96 times higher under LG, MG, and HG

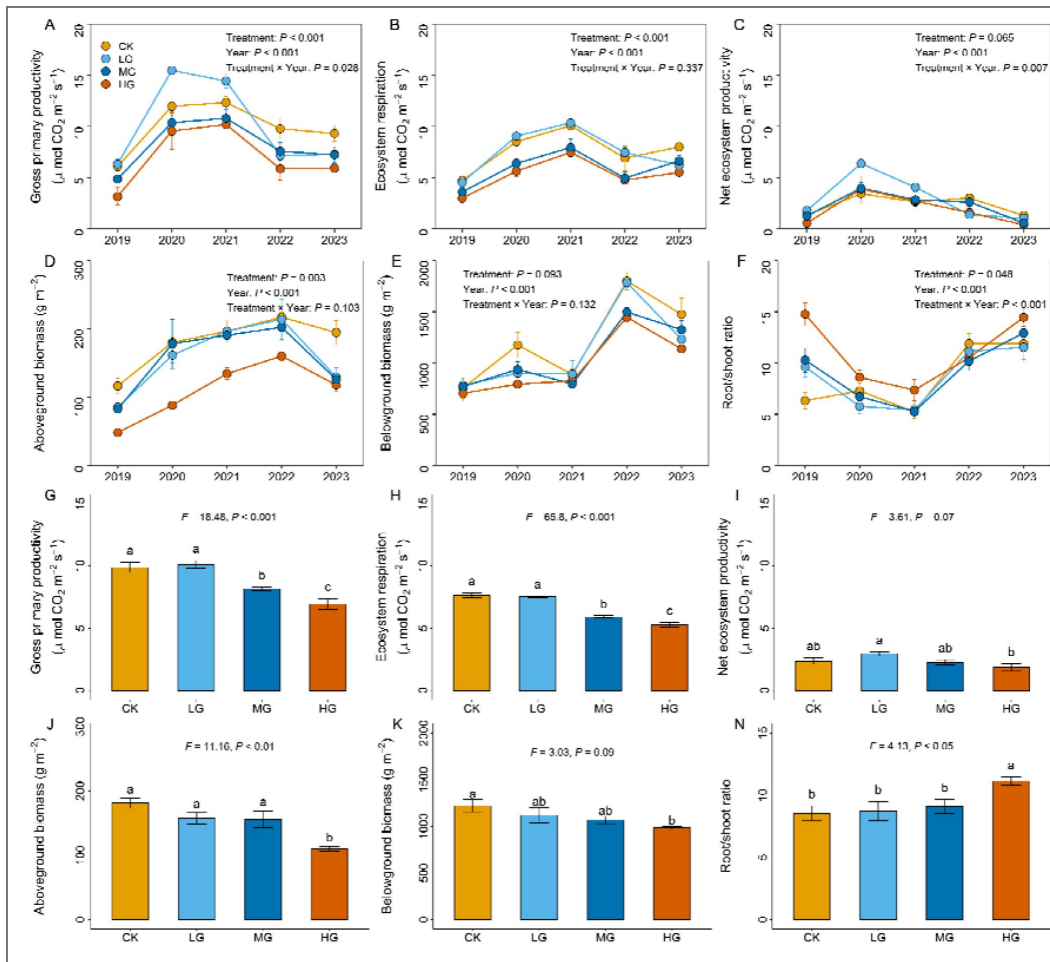


Figure 2. Effects of different grazing intensities on ecosystem carbon dioxide (CO₂) fluxes and biomass in our field experiment.

CK, enclosure; LG, light grazing; MG, moderate grazing; HG, heavy grazing. Data (means \pm SE, $n = 3$) followed by different lowercase letters indicate differences at $P < 0.05$ between treatments.

respectively, compared to CK (Fig. S5). The NEP increased with WI under HG (Fig. S6; $P < 0.01$), whereas the response ratio of NEP to heavy grazing was not significantly correlated with WI (Fig. 3B).

3.2 Synthesis of grazing on ecosystem CO₂ fluxes and plant biomass across global grasslands

In the meta-analysis across global grasslands, grazing significantly decreased ecosystem CO₂ fluxes by 13.56% to 30.46% (Fig. 4). Significant differences were observed in the responses of ecosystem CO₂ fluxes to different grazing intensities across global grasslands (Fig. 5A). Heavy grazing had a more pronounced negative effect on ecosystem CO₂ fluxes compared to light and moderate grazing. The response of GPP was decreased by 15.89%, 11.88% and 26.34%, respectively, under LG, MG and HG. The response of ER was decreased by 7.42%, 14.91% and 21.82%, respectively, under LG, MG and HG. The response of NEP was decreased by 18.86% and 34.89%, respectively, in LG and HG, but was not significant in MG. Light, moderate and heavy grazing resulted in reductions of AGB by 27.89%, 34.57% and 66.17% (Fig. 5B). Moderate and heavy grazing decreased the BGB by 14.85% and 26.13%, respectively, but the response of BGB was not significant in LG. Grazing increased the root shoot ratio by 31.78% to 111.11%. Heavy grazing had a more pronounced positive effect on root shoot ratio compared to light and moderate grazing.

Globally, grazing decreased GPP, ER and NEP under low precipitation conditions (≤ 400 mm), while the reductions were not significant under high precipitation conditions (> 400 mm) (Fig. S7A). Grazing significantly reduced GPP, ER, and NEP at mean annual temperatures ≤ 5 °C, but these effects were not significant at temperatures > 5 °C (Fig. S7B). Similarly, under lower wetness conditions ($WI \leq 30$), grazing decreased GPP, ER, and NEP more than under higher wetness conditions ($WI > 30$) (Fig. 6). The response of NEP was decreased under lower WI ($WI \leq 30$) in MG and HG, but it was not different under higher WI ($WI > 30$) in MG. The response of NEP was decreased under higher WI ($WI > 30$) in HG. Higher wetness index mitigated the response of NEP to grazing. The duration of grazing also influenced its effect: GPP and ER declined more substantially under longer grazing durations (Fig. S7C). The most pronounced decline in NEP occurred under grazing durations of 5 to 10 years ($P < 0.001$).

In global grasslands, the key environmental factors influencing GPP and ER response to grazing included WI, grazing duration, the response of soil moisture, and grazing intensity (Fig. S8; $P < 0.05$). For NEP, the major predictors were WI, grazing duration and intensity ($P < 0.05$). The most important environmental parameters for AGB response to grazing were grazing intensity, WI, grazing duration, the response of soil moisture and temperature and livestock types. For BGB, the major predictors were WI, grazing duration, the response of soil moisture and temperature. The response of NEP was positively correlated with WI under light, moderate and total grazing in global grasslands (Fig. 7; $P < 0.1$). The response of ecosystem CO₂ fluxes was affected by AGB under grazing in global grasslands (Fig. S9).

4. Discussion

4.1 The responses of ecosystem CO₂ fluxes and plant biomass to grazing and controlling factors

Grazing decreased the responses of ecosystem CO₂ fluxes and plant biomass in global grasslands, but only NEP was not significantly affected by grazing in our field experiment (Fig. 4 and S10). The lack of a significant response in NEP may be because the site in this field study was managed for year-round continuous low-intensity grazing (Liang et al., 2021). Grazing stimulated the NEP under wet conditions, but depressed it under dry conditions, a pattern consistent across the typical steppe in our experiment and supported by our global meta-analysis (Figs. 3B and 7H). This finding aligned with our first hypothesis (H1) that the response of NEP increased with the increase in wetness index under grazing. This relationship could be explained by the significant positive correlation of NEP with AGB (Fig. S9). The linear regression analysis also

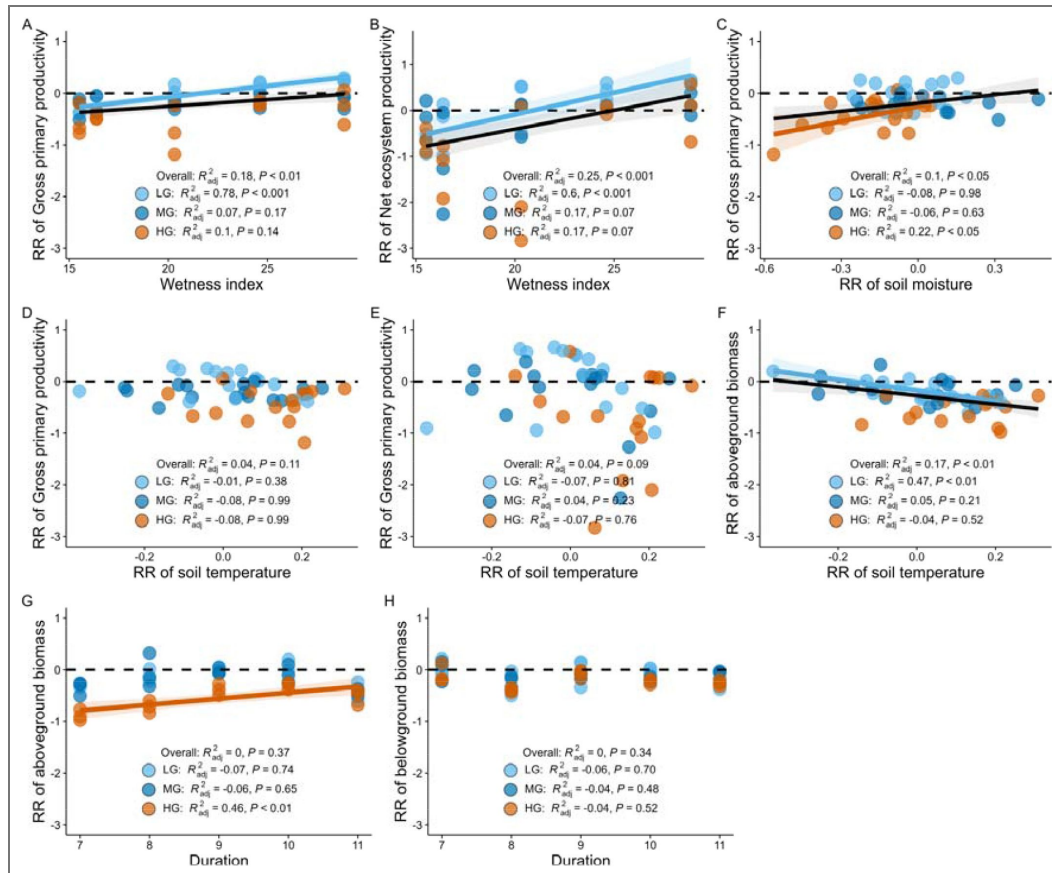


Figure 3. Relationships of the responses of gross primary productivity (GPP) and net ecosystem productivity (NEP) with potential regulating factors from 2019 to 2023 under different grazing intensity.

Overall, overall grazing; LG, light grazing; MG, moderate grazing; HG, heavy grazing. The significant regression lines and 95% confidence intervals are shown with lines (solid for significant) and shaded areas, respectively.

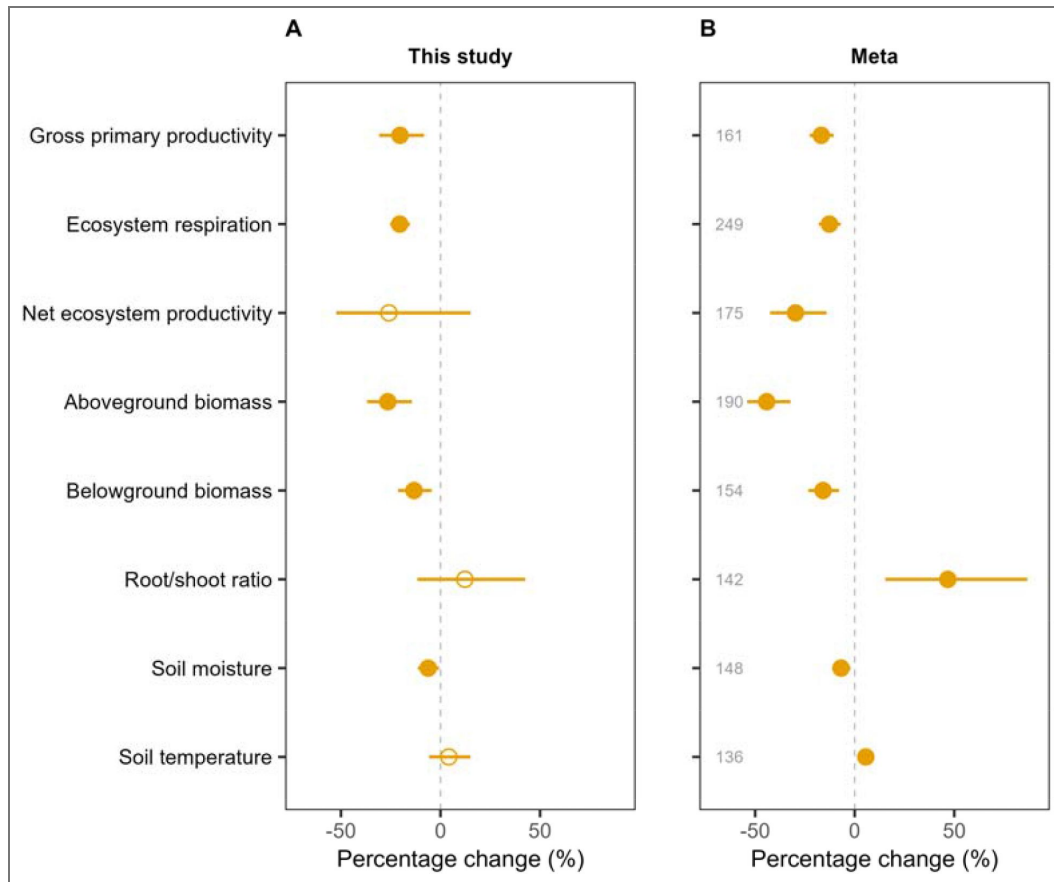


Figure 4. Effects of grazing on gross primary productivity, ecosystem respiration, net ecosystem productivity, aboveground biomass, belowground biomass and root shoot ratio, soil moisture and soil temperature, in global grasslands in the field experiment in this study (A) and from the meta-analysis (B).

Circles and error bars represent average parameter estimates and 95% confidence interval (CI). The star (*) indicates significance when the CI did not overlap zero. Sample sizes of observations for each variable are displayed on the left.

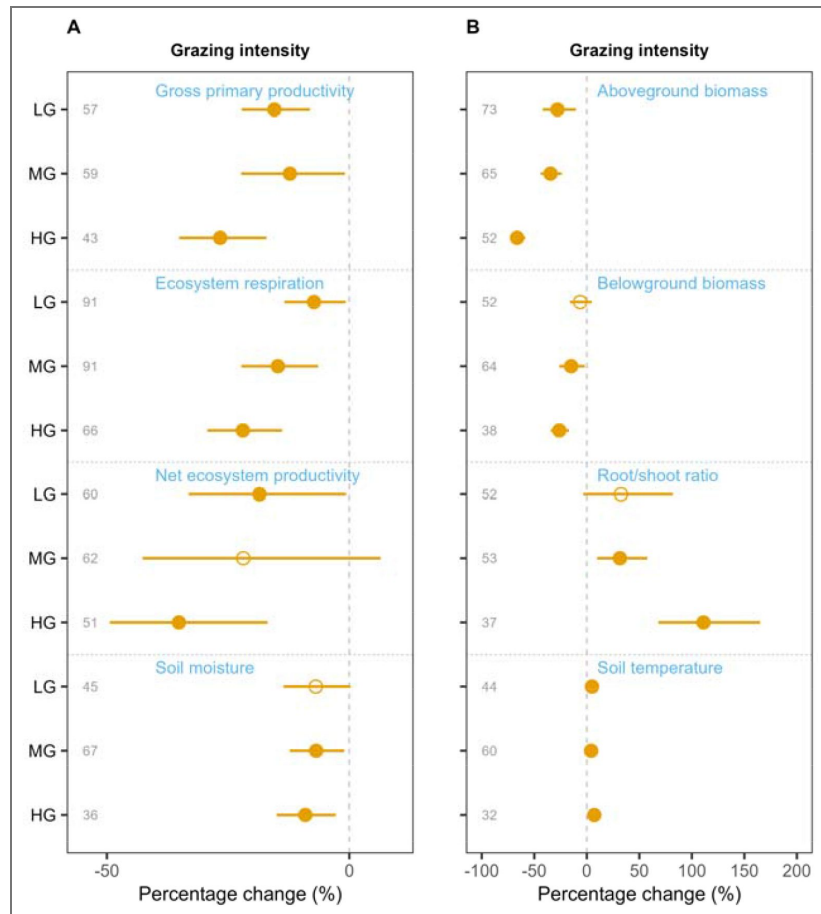


Figure 5. Effects of different grazing intensities on ecosystem CO₂ fluxes, biomass and soil temperature and moisture in global grasslands from the meta-analysis.

Circles and error bars represent average effects and their 95% confidence interval (CI). The star (*) indicates significant effects, i.e., the 95% CI did not overlap zero. The sample size for each variable is shown on the left. LG, light grazing; MG, moderate grazing; HG, heavy grazing.

Figure 6. Responses of ecosystem CO₂ fluxes and biomass to grazing (A) and different grazing intensities (B-C), at wetness index ≤ 30 and wetness index > 30 in global grasslands from the meta-analysis.

Circles and error bars represent average parameter estimates and 95% confidence interval (CI). The sample size for each variable is shown on the left. LG, light grazing; MG, moderate grazing; HG, heavy grazing.

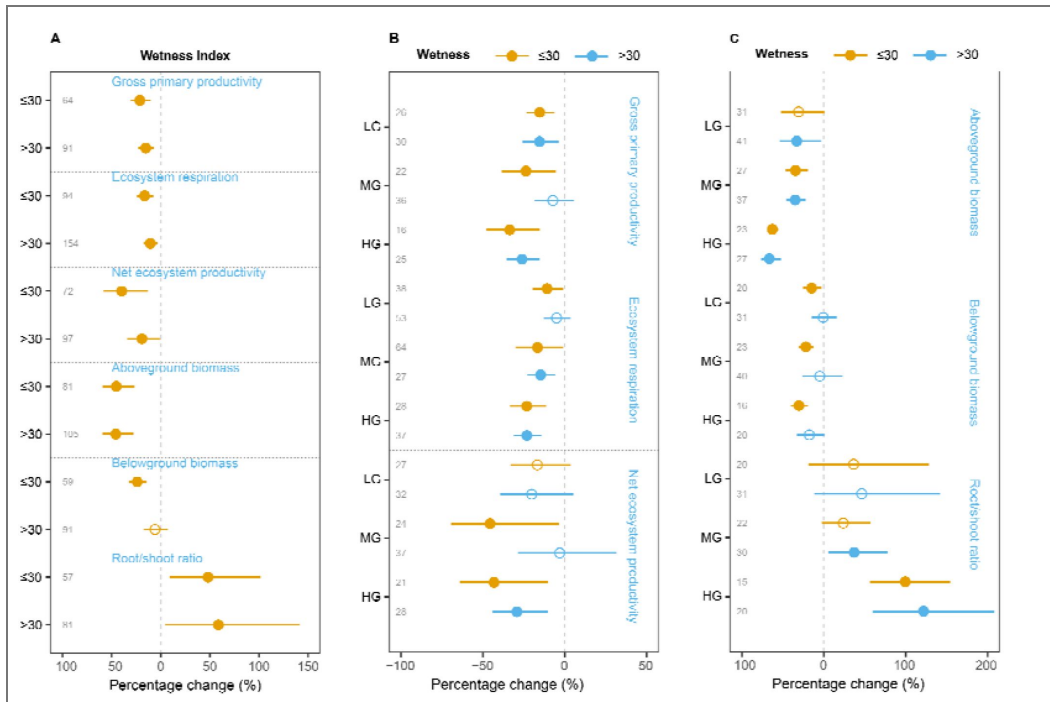
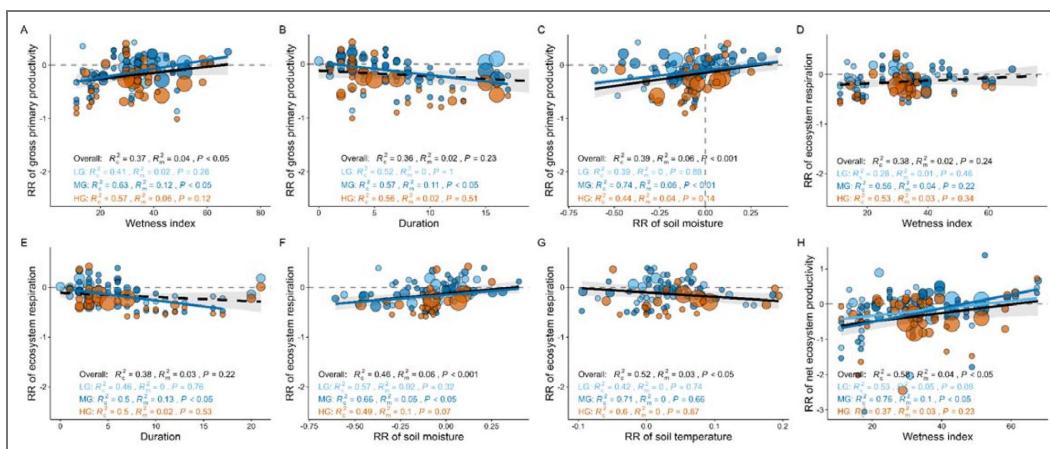


Figure 7. Relationships of the responses of ecosystem CO₂ fluxes with potential regulating factors in global grasslands from the meta-analysis.

The marginal (m) and conditional (c) R^2 indicate the proportion of variance explained by the fixed effects and by both the fixed and random effects study, respectively. The black solid lines and gray shaded areas in panels are the mean and 95% confidence interval of the slope, respectively. The sizes of points are proportional to their corresponding weights. RR, response ratio; overall, total grazing; LG, light grazing; MG, moderate grazing; HG, heavy grazing.



showed that light grazing stimulated the responses of NEP with increasing wetness index. This relationship could be explained by the significant positive correlation between NEP and both ANPP and RGR (Fig. S4). Light grazing usually stimulates leaf regrowth following defoliation, and these new leaves often are more physiologically active than the older leaves that contribute much of leaf area on ungrazed treatment (Wayne Polley et al., 2008). These new leaves likely imply a stronger leaf photosynthesis and C sink (Reich et al., 2007). Under lower wetness conditions ($WI \leq 30$), light grazing reduced GPP and ER to a lesser extent than moderate and heavy grazing (Fig. 6B). Compared with higher grazing intensities, light grazing consumed less forage by livestock, thereby better mitigated the impact of lower moisture on GPP and ER. Moderate grazing decreased the response of GPP and NEP under lower WI, but the response of GPP and NEP were not different under moderate grazing of higher WI in global grasslands (Figs. 6 and 8), indicating that higher wetness offset the response of GPP and NEP to moderate grazing. This was likely because grazing-induced biomass reduction was less under wet condition in grasslands (Jin et al., 2023). However, not all grazing intensities aligned with the first hypothesis, likely due to severe loss of vegetation resilience under heavy grazing. Heavy grazing, even under higher wetness, reduced NEP and AGB in global grasslands (Fig. 2, 5 and 6C), resulting in a severe decline or even loss of their resilience, which could not be restored to control levels in long-term heavy grazing (Irob et al., 2023).

Both our experiment and meta-analysis showed that aboveground biomass, grazing intensity and wetness index were key factors regulating the responses of ecosystem CO_2 fluxes to grazing (Fig. S3, S8 and S9), with their responses intensifying with higher aboveground biomass and wetness index, which aligned with our second hypothesis (H2). Grazing reduced aboveground biomass and plant respiration, thereby decreasing GPP and ER (Fig. 4; Fig. S10; Liu et al., 2020; Wang et al., 2025). Plants enhanced photosynthetic structures and physiological functions under grazing pressure. These adaptations improved CO_2 assimilation and allocate more carbohydrates to compensate for the loss of aboveground biomass, thereby achieving compensatory growth (Wang et al., 2020; Yu et al., 2025). The increase in GPP and NEP in LG in 2020 was due to the increased relative growth rate in LG than in CK (Fig. S5), suggesting that grazing stimulated greater plant compensatory growth in years with more precipitation (Li et al., 2025). Moreover, appropriate grazing intensity facilitated the removal of senescent plant tissues, leading to increased leaf light capture capability and enhanced community photosynthetic capacity (Shen et al., 2019). The aboveground and belowground biomass, as well as root shoot ratio of plants were influenced by grazing activities such as feeding, trampling, and excretion (Cao et al., 2024). In this study, plant biomass (both aboveground and belowground biomass) was lower under heavy grazing. Under heavy grazing conditions, where soil nutrients were often depleted, plants tended to prioritize biomass allocation to roots to enhance nutrient acquisition and utilization (Liu et al., 2024). Moreover, heavy grazing can stimulate C allocation to roots (Ren et al., 2024), which explains why the root/shoot ratio was higher under heavy grazing (Fig. 2). In the wetter years (2020 and 2021), the aboveground biomass was higher while the root shoot ratio was lower than in the drier years. Heavy grazing affected the allocation strategy of aboveground and belowground biomass by plants.

4.2 Limitations and implications for future study

Our results highlight that light grazing serves as a promising management strategy to promote aboveground net primary productivity and CO_2 sequestration. However, some aspects still need to be further explored. Our study has limitations due to the relatively small sample size, which stems from the scarcity of global-scale studies exploring the effects of grazing intensity on ecosystem CO_2 fluxes. The data of ecosystem CO_2 fluxes from large-scale eddy covariance flux towers were not included in this meta-analysis, because there is an absence of a robust model to convert data between flux tower observations and chamber-based methods (Shi et al., 2022b). In addition, future studies could conduct more experiments of ecosystem CO_2 fluxes in South American, Africa and Oceania, which have large amounts of grasslands for grazing.

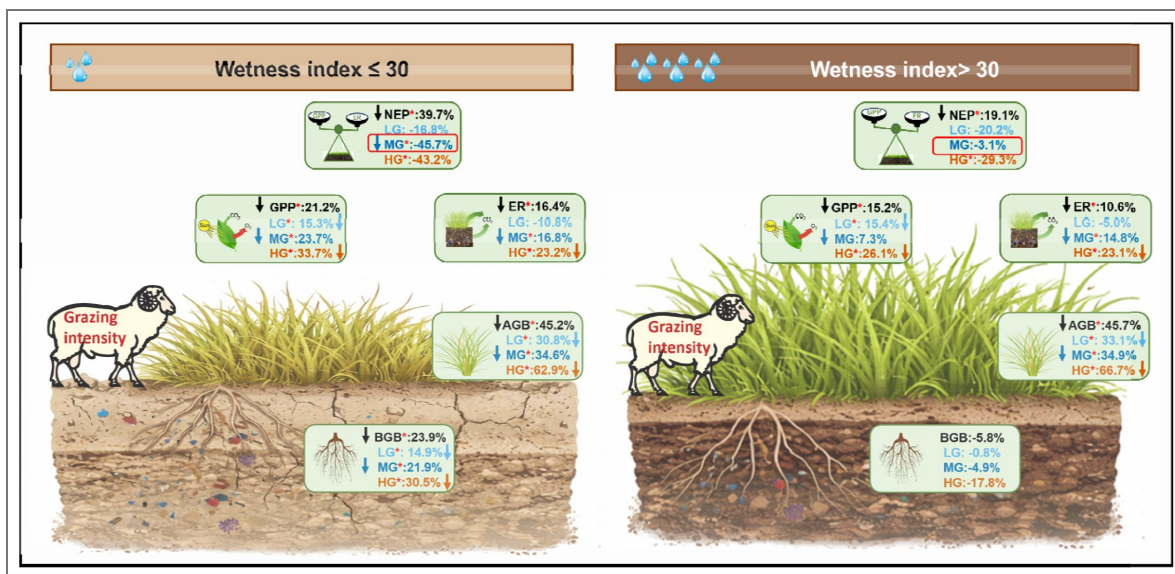


Figure 8. Schematic summary of the effects of grazing intensity on ecosystem carbon dioxide (CO₂) fluxes and biomass in global grasslands in the meta-analysis.

The arrows indicate negative effects. Asterisks (*) indicate significant effects on variables at $P < 0.05$. GPP, gross primary productivity; ER, ecosystem respiration; NEP, net primary productivity; LG, light grazing; MG, moderate grazing; HG, heavy grazing.

Regardless of these limitations, our study has significant implications for future study and grassland production. The primary factors regulating ecosystem CO₂ flux responses to grazing were identified as aboveground biomass, wetness index and grazing intensity. The NEP was positively affected by wetness index in LG, MG and HG. However, in both the typical steppe grazing experiment and the synthesis of global grasslands, the NEP resilience increased with higher wetness index specifically under light grazing, but not under heavy grazing. During wetter years, the NEP was even higher under LG compared to CK, whereas in drier years, no significant difference was observed between LG and CK (Fig. 2 [↗](#)). This pattern aligns with the greater RGR and ANPP observed under elevated wetness index in light grazing treatment (Fig. S4). Globally, higher wetness index and aboveground biomass enhanced the response of NEP to grazing (Figs. 3 [↗](#), 7 [↗](#) and S9). However, even under higher wetness conditions, heavy grazing reduced NEP and AGB in global grasslands (Fig. 6 [↗](#)), reflecting a severe decline, or even loss of resilience under long-term heavy grazing pressure. These results indicate that the negative impacts of long-term heavy grazing on NEP could not be offset by higher annual wetness index in global grasslands, underscoring the necessity of implementing strict grazing management measures. Additionally, moderate grazing under wetter years may be an appropriate management strategy to sustain grassland carbon balance while supporting livestock production.

In summary, this study presents the first comprehensive assessment of how annual wetness index affecting the response of ecosystem CO₂ fluxes to grazing across global grasslands. Our results showed that wetness index and aboveground biomass were key factors regulating the responses of ecosystem CO₂ fluxes, and both exhibiting positive associations with these responses. Grazing reduced the response of GPP and ER in our field experiment of typical steppe and in the meta-analysis of global grasslands. Higher wetness indices offset the effect of moderate grazing rather than heavy grazing on NEP in global grasslands. These findings underscore the importance of developing region-specific grazing strategies guided by local wetness indices.

Data availability

Data will be available on request.

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Additional files

[Supplementary materials](#) [↗](#)

Additional information

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Peer reviews

Reviewer #1 (Public review):

Summary:

This study examines whether gaze direction actively shapes choice during food preference decisions or whether gaze and choice evolve largely independently until the moment of commitment. The established framework in this context, the aDDM, assumes that gaze

causally biases the accumulation of evidence in favour of the fixated item. The authors show convincingly that this model fails to fit key behavioural patterns across several datasets, as do other published models that make the same assumption. The authors propose an alternative model (Post-Decision-Gaze or PDG) in which gaze and decision formation are decoupled: gaze does not influence the decision process, nor is it drawn toward the ultimately chosen item, until after the decision threshold is reached. Only during the motor execution period (after commitment) is gaze directed to the chosen option. They demonstrate that this model fits several observed patterns better than the aDDM and related variants.

Strengths:

The work thoroughly considers multiple models and datasets. It advances an interesting alternative perspective on gaze-decision interactions and highlights meaningful shortcomings in existing models. The authors take the time to explain how modelling assumptions produce specific patterns in the data, which is certainly insightful to readers interested in the modelling of value-based decision making.

Weaknesses:

It is unclear to what extent the model's success relies on the way non-decision time is formalised in the model. In the proposed PDG model, non-decision time is decomposed into separate visual encoding, saccadic execution, and manual execution components. Several values (assumed or recovered) do not match known physiological or behavioural ranges. This is a common issue in the literature, and the authors may want to address it in light of broader work discussing what non-decision time consists of in both manual and saccadic actions (e.g., Bompas et al., 2024, Non decision time: the Higgs boson of decision, *Psychological Review*).

In particular, the "saccadic execution" parameter appears far too long and too variable to reflect merely execution; instead, it likely includes decisional components. This would make more sense since manual and saccadic planning essentially rely on distinct brain areas, hence it seems unrealistic that crossing a single threshold would trigger both manual and saccadic execution. Similarly, recovered manual non-decision times are substantially longer (though not more variable) than expected motor execution durations for button presses. These patterns suggest that parts of what the model treats as non-decision time are likely decisional in nature, although perhaps related to "action decision" rather than the "value-based decision" of interest to the authors. To what extent these two processes neatly follow each other or overlap could be usefully considered.

<https://doi.org/10.7554/eLife.110725.1.sa2>

Reviewer #2 (Public review):

Summary:

Zylberberg et al. reanalyze eye-tracking and behavioral data (mostly from Krajbich et al., 2010) to test two predictions of the attentional Drift Diffusion Model, finding that these predictions are not met. Similarly, predictions of normative models (inspired by rational inattention) are not in line with the data, and the authors propose a post-choice model of attention. This model better accounts for the two effects but also does not account for all patterns, so the authors conclude that eye movements most likely reflect both pre- and post-decisional processes.

Strengths:

A clear strength is the systematic falsification-based approach of the paper, establishing (partially) new predictions and testing to what extent these are met by extant models and by a newly developed theory. The authors do a good job in providing intuitions behind the

effects and the reasons why models such as the aDDM predict them. The paper is of substantial relevance for the field, as it shows that effects pertaining to the last fixation(s) should be interpreted with caution. Another strength is the paper's transparency as the authors clearly acknowledge that their new model does not do a perfect job either.

Weaknesses:

The paper focuses on analyzing the Krajbich 2010 data, but shows that the second effect replicates in many other datasets. A more principled approach, in which both effects are analyzed and presented for all datasets, would be more convincing. The results should then be shown together for clarity/readability.

Similarly, it would be nice to show to what extent the models' predictions depend (not depend) on using the best-fitting parameter values (are there any parameter settings under which the two effects are not predicted?)

<https://doi.org/10.7554/eLife.110725.1.sa1>

Reviewer #3 (Public review):

Summary:

In this study, the authors reanalyzed choice, RT and gaze datasets collected from human subjects performing a food-choice task. They show that models that posit a causal role for attention in shaping the decision-making process fail to account for empirical observations in the data. These include the attentional drift diffusion model (aDDM) and models that derive attention-choice associations from an optimal policy. The authors show that a model that assumes that gazes are directed towards the chosen option after decision commitment captures more (but not all) empirical findings, suggesting that attention may reflect decisions once they are made instead of contributing to their formation. However, this post-decision-gaze (PDG) model failed to capture all aspects of the data, suggesting that gaze may reflect both decisional and post-decisional operations, and existing models are still missing some features of the gaze-directing process. The authors provide convincing evidence that post-decision gaze explains a number of empirical findings in this task.

Strengths:

- (1) The analyses are generally appropriate, and the conclusions are supported by the data.
- (2) The study was rigorous, as the authors considered a number of alternative possible models for behavior, and evaluated their performance based on a wide range of qualitative predictions (as opposed to exclusively relying on model comparison).
- (3) The proposal that gaze may largely reflect post-decisional processes is interesting, and as far as I am aware, novel.

Weaknesses:

There was limited discussion about why one might allocate attention post-decision. I would have appreciated more discussion on the potential functional consequences or implications of post-decision gaze.

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